

# Strouhal numbers and optimization of swimming by odontocete cetaceans

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## Summary

Swimming efficiencies of fish and cetaceans have been related to a certain synchrony between stroke cycle frequency, peak-to-peak tail/fluke amplitude and mean swimming speed. These kinematic parameters form a non-dimensional wake parameter, referred to as a Strouhal number, which for the range between 0.20 and 0.40 has been associated with enhanced swimming efficiency for fish and cetaceans. Yet to date there has been no direct experimental substantiation of what Strouhal numbers are preferred by swimming cetaceans. To address this lack of data, a total of 248 Strouhal numbers were calculated for the captive odontocete cetaceans *Tursiops truncatus*, *Pseudorca crassidens*, *Orcinus orca*, *Globicephala melaena*, *Lagenorhynchus obliquidens* and *Stenella frontalis*. Although the average Strouhal number calculated for each species is within the accepted range, considerable scatter is found in the data both within species and among individuals. A greater proportion of Strouhal values occur between 0.20 and 0.30 (74%) than the 0.25–0.35 (55%) range predicted for maximum swimming efficiency. Within 0.05 Strouhal increments, the greatest number of Strouhal values was found between 0.225 and 0.275 (44%).

Where propulsive efficiency data were available (*Tursiops truncatus*, *Pseudorca crassidens*, *Orcinus orca*), peak swimming efficiency corresponded to this same Strouhal range. The odontocete cetacean data show that, besides being generally limited to a range of Strouhal numbers between 0.20 and 0.40, the kinematic parameters comprising the Strouhal number provide additional constraints. Fluke-beat frequency normalized by the ratio of swimming speed to body length was generally restricted from 1 to 2, whereas peak-to-peak fluke amplitude normalized by body length occurred predominantly between 0.15 and 0.25. The results indicate that the kinematics of the propulsive flukes of odontocete cetaceans are not solely dependent on Strouhal number, and the Strouhal number range for odontocete cetaceans occurs at slightly (~20%) lower values than previously predicted for maximum swimming efficiency.

Key words: Strouhal number, swimming, dolphin, cetacean, odontocete, *Tursiops*, *Pseudorca*, *Orcinus*, *Lagenorhynchus*, *Globicephala*, *Stenella*, *Delphinapterus*.

## Introduction

An important aspect of swimming is the ability to move efficiently. Paradoxically, early attempts at building fish-inspired mechanisms achieved disappointingly low efficiencies (Triantafyllou and Triantafyllou, 1995). It was only through a deeper understanding of the vorticity produced along the swimming animal and in its wake that significant progress was achieved. Beginning almost 40 years ago, Rosen (1959, 1961, 1963) discerned, through a series of innovative flow visualization experiments, a system of vortices appearing along the sides of swimming fish and dolphins. Rosen (1959, 1961, 1963) hypothesized that some of the rotational energy surrounding the undulating motion of a fish or dolphin could be regained for propulsion through proper synchronization of the animal's body to the vortex flow. Rosen (1959, 1961) further deduced an equation for fish and dolphin motion. This equation predicted swimming speed to be proportional to the product of the tail beat amplitude and frequency. Rosen (1959,

1961) referred to this proportionality as the 'fish' constant and hypothesized that it was nearly the same for fish and dolphins.

A similar conclusion, but through more rigorous theoretical analysis and detailed experimental studies, has been drawn by Triantafyllou et al. (1991, 1993). Performing stability analysis of the mean velocity profiles of a pitching airfoil, Triantafyllou et al. (1991, 1993) have shown that maximum spatial amplification and optimum creation of thrust-producing jet vortices lies in a narrow range of nondimensional frequencies referred to as the Strouhal number ( $St$ ). The predicted  $St$  range for maximum spatial amplification occurs between 0.25 and 0.35, peaking at 0.30 (Triantafyllou et al., 1991, 1993; Streitlien and Triantafyllou, 1998). Triantafyllou and Triantafyllou (1995) have argued that for  $St=0.25-0.35$ , swimming efficiency for fish and cetaceans would also peak. Experiments with isolated oscillating foils have found highest propulsive efficiencies for  $St$  between 0.20 and 0.40

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(Triantafyllou et al., 1991, 1993, 2000; Anderson et al., 1998; Read et al., 2003).

The  $St$ , which is related to how fast the vortices are being generated and the space between them, is defined as:

$$St = Af/U, \quad (1)$$

where  $A$  is the width of the wake, taken to be equal to the peak-to-peak maximum excursion of the trailing edge of the foil or fluke,  $f$  is the frequency of oscillation, and  $U$  is the mean forward velocity.  $St$  is in fact the inverse of the 'fish' constant. Similar combinations of these kinematic swimming parameters have previously been made to characterize the swimming motion of fish (e.g. Rosen, 1959, 1963; Pyatetskiy, 1970; Webb, 1975), cetaceans (Semonov et al., 1974; Kayan and Pyatetskiy, 1977) and athletes (Pershin, 1988), but not within such a predictive theoretical framework.

Although many species of cetaceans are believed to be particularly swift, efficient swimmers, corresponding  $St$  data have been extremely limited. The cetacean Strouhal number data of Triantafyllou et al. (1993) consist of only two values. Moreover, they were indirectly derived from analysis of traces (Lang and Daybell, 1963) obtained from motion picture frames of a 2.03-m Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) swimming non-uniformly within a tank. One  $St$  value, 0.32, corresponded to the dolphin swimming while wearing a 1.91 cm-diameter drag collar. The remaining  $St$  of 0.30 corresponded to swimming without the drag collar. References to this less than optimal data set (Triantafyllou et al., 1991, 1993, 2000; Triantafyllou and Triantafyllou, 1995; Taylor et al., 2003) appear repeatedly throughout the literature.

Many different species of captive odontocete cetaceans have been trained to swim steadily behind viewing panels and provide a unique opportunity for a much larger, more accurate  $St$  database. Here, Strouhal numbers are calculated from recordings of six species of trained odontocete cetaceans. The species include members of the family Delphinidae: bottlenose dolphin (*Tursiops truncatus*), false killer whale (*Pseudorca crassidens*), spotted dolphin (*Stenella frontalis*), striped dolphin (*Lagenorhynchus obliquidens*), killer whale (*Orcinus orca*) and pilot whale (*Globicephala melaena*). For comparison, Strouhal numbers for the slower, less efficient swimming beluga whale (*Delphinapterus leucas*; family Monodontidae) are also included but treated separately.

The objective of the present study was to investigate the range of Strouhal numbers preferred by swimming cetaceans, how this range varied between species, within species and for individuals and, most critical, what range of Strouhal numbers corresponded to maximum propulsive efficiency. Data directly relating swimming efficiency to  $St$ , for any swimming animal, have previously not existed (Bandyopadhyay et al., 2000).

## Materials and methods

### Experimental animals

The swimming motions of seven species of trained odontocete whales were recorded at Sea World in Orlando, FL,

USA, San Antonio, TX, USA and San Diego, CA, USA and the National Aquarium in Baltimore, MD, USA. The species examined were from the family Delphinidae, including one spotted dolphin (*Stenella frontalis* Cuvier), two Pacific white-sided dolphins (*Lagenorhynchus obliquidens* Gill), 11 bottlenose dolphins (*Tursiops truncatus* Montagu), four false killer whales (*Pseudorca crassidens* Owen), one pilot whale (*Globicephala melaena* Lesson) and six killer whales (*Orcinus orca* Linnaeus), and the family Monodontidae, including three beluga whales (*Delphinapterus leucas* Pallus). Some of the data were previously reported in Fish (1993, 1998). Morphological measurements for each animal can be found in Table 1. Body length,  $L$ , is defined as the linear distance from the rostral tip to the fluke notch. The animals subsisted on a diet of herring, smelt, mackerel and squid supplemented with vitamins, dispersed at irregular intervals throughout the day.

Experiments were performed in large elliptical pools with maximum lengths of 27.4–48.8 m. The curved portions of each pool were constructed of 1.7–2.1 m-wide Plexiglas panels separated by 0.2 m-wide posts, allowing for an unobstructed view of the animals as they swam. A water depth of 1.4–2.1 m was visible through the panels. The depth of the pools was

Table 1. Morphometrics of odontocete cetaceans

Species	Sex	Body mass (kg)	Body length (m)	Age (years)
<i>Stenella frontalis</i>	Male	81.6	1.83	5
<i>Lagenorhynchus obliquidens</i>	Male	130.6	2.18	16
<i>Lagenorhynchus obliquidens</i>	Female	139.7	2.25	15
<i>Tursiops truncatus</i>	Female	146.9	2.49	4
<i>Tursiops truncatus</i>	Male	149.2	2.06	3.5
<i>Tursiops truncatus</i>	Female	187.8	2.57	17
<i>Tursiops truncatus</i>	Female	192.8	2.51	20
<i>Tursiops truncatus</i>	Male	211.4	2.54	18
<i>Tursiops truncatus</i>	Female	212.3	2.59	8.5
<i>Tursiops truncatus</i>	Female	219.1	2.69	16
<i>Tursiops truncatus</i>	Male	228.2	2.70	20
<i>Tursiops truncatus</i>	Female	229.5	2.60	20
<i>Tursiops truncatus</i>	Female	256.3	2.95	13
<i>Tursiops truncatus</i>	Female	263.1	2.70	22
<i>Pseudorca crassidens</i>	Female	358.3	3.57	9
<i>Pseudorca crassidens</i>	Female	391.3	3.71	10
<i>Pseudorca crassidens</i>	Female	508.1	3.88	8
<i>Pseudorca crassidens</i>	Male	762.9	3.99	8
<i>Delphinapterus leucas</i>	Male	589.7	3.56	12
<i>Delphinapterus leucas</i>	Female	698.5	3.25	8
<i>Delphinapterus leucas</i>	Male	725.7	4.12	13
<i>Globicephala melaena</i>	Female	764.3	3.99	15
<i>Orcinus orca</i>	Male	841.9	3.81	1.8
<i>Orcinus orca</i>	Female	929.9	4.16	3
<i>Orcinus orca</i>	Female	1424.3	4.46	16
<i>Orcinus orca</i>	Female	1995.8	5.16	16
<i>Orcinus orca</i>	Female	2086.5	5.57	16
<i>Orcinus orca</i>	Female	2331.5	5.25	10

7.3–11.0 m, and water temperature ranged between 12°C and 22°C.

The animals normally swam about 0.5–1.0 m below the surface of the water and 1 m from the pool walls. Many of the animals were trained to perform ‘fast swims’ around the circumference of the main performance pool, thereby providing a larger range of swim speeds to study. Initial training involved instructing the animals to accelerate quickly and touch their rostrum to a boat pole held several meters in front of them. Through successive approximations of positioning the boat pole further and further away, the dolphins were trained to swim fast upon command. When the dolphins were not swimming at what the trainers judged to be peak performance, the boat pole was slapped on the surface of the water to induce the dolphins to swim more rapidly. Trainers frequently raced animals in pairs to provide additional incentive. A wide variety of rewards, including tactile stimulation, environmental enrichment devices and food, were given for appropriate behaviors on an intermittent reinforcement schedule. In addition to performing in shows, the dolphins in this study participated in training, play, relationship, husbandry and exercise sessions on a regular basis. Approximately 18–20 h of their day consisted of nonstructural play, free and rest time.

#### Video analysis

A camcorder (Sony CCD-TR81 or Panasonic DV-510) was used to record swimming sequences of cetaceans at a rate of 30 frames s<sup>-1</sup>. The camcorder was positioned in front of the Plexiglas wall of the pool, allowing for a clear view of three panels. Swimming motions of the animals were recorded as they routinely swam and when they were encouraged to swim at maximum speed. Sequential body and fluke positions were determined directly from individual frames of videotape with a Panasonic AG-7300 video recorder and video monitor or were digitized using the Peak Motus video analysis system (version 4.3.1; Peak Performance Technologies, Englewood, CO, USA). Kinematic data from video records to calculate Strouhal number included mean swimming speed ( $U$ ; m s<sup>-1</sup>), fluke oscillation frequency ( $f$ ; Hz) and peak-to-peak fluke amplitude ( $A$ ; m).  $A$  is defined as the maximum vertical displacement of the trailing edge of the flukes. Only video sequences in which the animals appeared to be swimming horizontally and at a constant speed were used.

At Sea Worlds in Orlando and San Antonio, the animals were marked with zinc oxide reference points on the lateral aspects of the caudal peduncle. Marks were separated by a measured distance of 0.1–0.39 m and served as the scale for video analysis. At the San Diego site, the animals were not marked. The scale was determined from a marked section of the Plexiglas panels of the pool.  $U$  was determined by dividing the length of a marked section through which the dolphin swam by the time that it took the dolphin to swim across it. Time was determined from the frame rate. Dolphin swimming speed measurements obtained from the video could be accurately repeated to within a few percent. This uncertainty resulted

from the fact that time was quantified by the frame rate, so crossing points could be off by a fraction of a frame rate. At the highest speeds of 8 m s<sup>-1</sup>, the 8 m run resulted in 30 frames between start and finish, of which the last two frames were suspect. This could result in, at most, a 7% uncertainty (two frames out of 30).

To assess if the Plexiglas panels and the recording position affected the calculations of  $U$ , video recordings of a cast model of a dolphin dorsal fin were made as it was moved along the normal swimming trajectory of the animals. The difference in distance between the actual positions where the cast fin crossed the reference marks and that determined from the video recordings was insignificant.  $f$  was calculated by dividing the frame rate by the number of frames comprising a single complete oscillation of the tail. Again, the frame rate limited accuracy for determining the tail oscillation period. For a relatively high frequency of 3 Hz, the period was determined from 10 frames. With a full frame ambiguity at each end of the oscillation the uncertainty would be, at most, 20%. The peak-to-peak amplitude of the fluke,  $A$ , along with a previously measured reference length marked on the tank wall, was measured directly on the television monitor screen. The reference length was recorded inside and outside the pool to account for refraction effects. The reference length provided a means of converting lengths measured on the monitor screen to actual distances in meters. The spatial resolution of the fluke at maximum and minimum amplitude is, as for the swim speed measurements, affected by the framing rate of the camera. However, because the fluke tip is moving relatively slowly at these extremes, the majority of the amplitude uncertainty resulted from resolving on the video screen the position of the tip of the fluke, particularly if the fluke was close to the water's surface. When Strouhal number

Table 2. Regression equations for kinematics

Species	Regression equation	$r^2$
<i>Delphinapterus leucas</i>	$f=0.136+1.462U/L$	0.861
$n=3$	$A/L=0.226-0.034U/L$	0.317
<i>Globicephala melaena</i>	$f=2.246-0.112U/L$	0.318
$n=1$	$A/L=0.086+0.056U/L$	0.113
<i>Lagenorhynchus obliquidens</i>	$f=-0.484+1.256U/L$	0.318
$n=2$	$A/L=0.132+0.030U/L$	0.077
<i>Orcinus orca</i>	$f=0.890+0.615U/L$	0.529
$n=6$	$A/L=0.179+0.024U/L$	0.066
<i>Pseudorca crassidens</i>	$f=0.368+1.056U/L$	0.642
$n=4$	$A/L=0.160+0.026U/L$	0.095
<i>Stenella frontalis</i>	$f=0.408+1.131U/L$	0.829
$n=1$	$A/L=0.248-0.001U/L$	0.002
<i>Tursiops truncatus</i>	$f=0.624+0.844U/L$	0.760
$n=11$	$A/L=0.624+0.844U/L$	0.097
Pooled $f$	$f=0.585+0.885U/L$	0.802
Pooled $A/L$	$A/L=0.184+0.015U/L$	0.091
$n=28$		

$f$ , frequency of propulsive cycle;  $A/L$ , length-specific peak-to-peak amplitude;  $U/L$ , length-specific swimming speed.

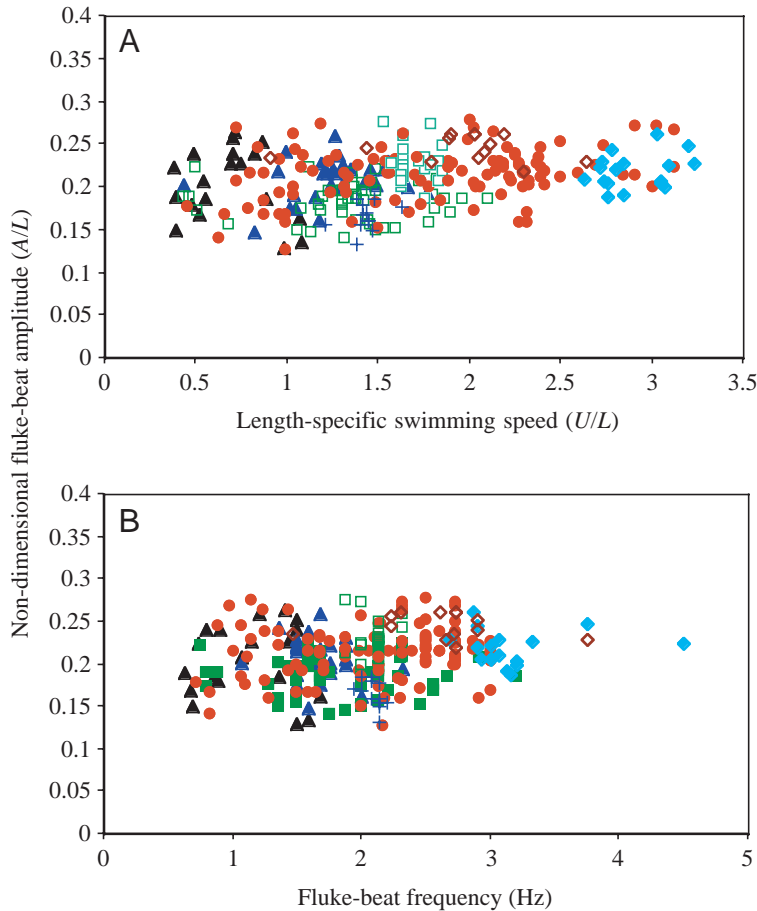
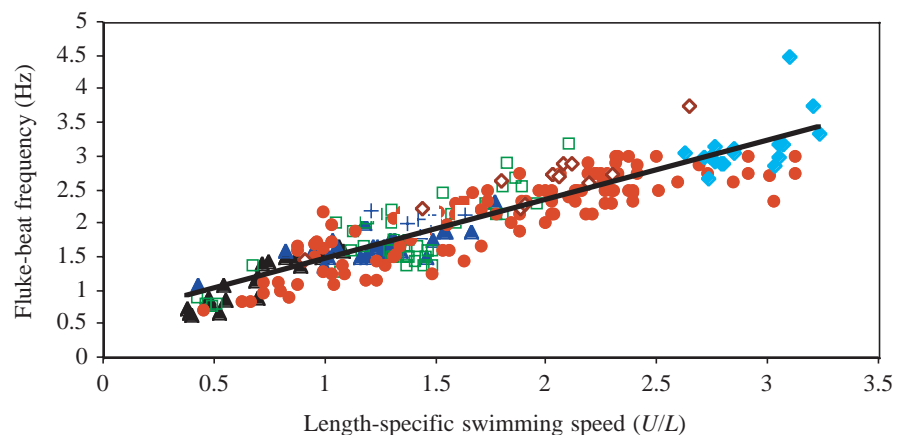


Fig. 1 (A) Non-dimensional fluke-beat amplitude,  $A/L$ , as a function of length-specific swimming speed,  $U/L$ , where  $A$  is the peak-to-peak fluke-beat amplitude,  $L$  is the body length and  $U$  is the swimming speed. (B) Non-dimensional fluke-beat amplitude,  $A/L$ , as a function of fluke-beat frequency  $f$  (Hz), where  $A$  is the peak-to-peak fluke-beat amplitude and  $L$  is the body length. Symbols indicate particular cetacean species: *Tursiops truncatus* (solid red circles), *Pseudorca crassidens* (open green squares), *Orcinus orca* (solid blue triangles), *Globicephala melaena* (blue crosses), *Lagenorhynchus obliquidens* (solid blue diamonds), *Stenella frontalis* (open brown diamonds) and *Delphinapterus leucas* (solid black triangles).

Fig. 2. Fluke-beat frequency,  $f$  (Hz), as a function of length-specific swimming speed,  $U/L$ , where  $L$  is the body length and  $U$  is the swimming speed. Regression equation for all the cetacean data is:  $y = 0.89x + 0.59$  ( $r^2 = 0.8$ ,  $N = 267$ ). Symbols indicate particular cetacean species: *Tursiops truncatus* (solid red circles), *Pseudorca crassidens* (open green squares), *Orcinus orca* (solid blue triangles), *Globicephala melaena* (blue crosses), *Lagenorhynchus obliquidens* (solid blue diamonds), *Stenella frontalis* (open brown diamonds) and *Delphinapterus leucas* (solid black triangles).



calculations were repeated for the same recordings but by independent observers, swimming speed and tail beat frequencies showed excellent agreement; for tail beat amplitudes, differences of 10–20% were not uncommon. This uncertainty resulted from insufficient screen resolution, framing rate and the proximity of the tail to the water surface. Overall  $St$  uncertainty was estimated to be  $\sim 20\%$ . This is 6% less than the  $St$  uncertainty calculated for the worse case scenario by propagating the independent uncertainties estimated for high speeds (7%), high frequencies (20%) and a fluke amplitude uncertainty of 15%.

To adjust for size differences between species, data were analyzed with respect to length-specific velocity ( $U/L$ ) and length-specific amplitude ( $A/L$ ). In some analyses,  $f$  was non-dimensionalized by dividing frequency by  $U/L$ . Means were calculated for values that did not vary with  $L$  or  $U/L$ . Variation about means was expressed as  $\pm 1$  s.d. Linear relationships were estimated by least-squares regression (Microsoft Excel). Differences in slopes of the regressions were analyzed by analysis of covariance (Zar, 1984). Means of species were compared using analysis of variance (ANOVA; Statistica Version 4.1, StatSoft). Results were considered significant at the  $\alpha = 0.05$  level.

## Results

### Kinematic data

A total of 267 swimming sequences were used for kinematic analysis (*S. frontalis*,  $n = 13$ ; *L. obliquidens*,  $n = 17$ ; *T. truncatus*,  $n = 107$ ; *P. crassidens*,  $n = 69$ ; *G. melaena*,  $n = 12$ ; *O. orca*,  $n = 30$ ; *D. leucas*,  $n = 19$ ). The animals maintained continuous propulsive motions by vertical oscillations of the flukes, as has been described previously (Fish, 1993, 1998; Rohr et al., 2002). The fastest mean swimming speeds were  $U = 6.42 \pm 0.41 \text{ m s}^{-1}$  and  $U/L = 2.90 \pm 0.19 \text{ L s}^{-1}$  for *L. obliquidens* and the slowest mean speeds were  $U = 2.38 \pm 0.74 \text{ m s}^{-1}$  and  $U/L = 0.68 \pm 0.22 \text{ L s}^{-1}$  for *D. leucas*.



With no statistically significant correlation,  $A/L$  was found to be relatively insensitive to both  $U/L$  (Fig. 1A) and  $f$  (Fig. 1B) for all species. The mean value of  $A/L$  for all odontocetes was  $0.21 \pm 0.03$  ( $n=267$ ). Mean  $A/L$  ranged from  $0.25 \pm 0.02$  for *S. frontalis* to  $0.17 \pm 0.02$  for *G. melaena* with 89% of the data residing between 0.15 and 0.25. ANOVA showed that there was a significant difference for  $A/L$  among species ( $P < 0.001$ ;  $F=9.76$ ; d.f.=6, 260). Aggregating all the odontocete data ( $n=267$ ),  $f$  was found to increase linearly with increasing  $U/L$  as  $f=0.89(U/L)+0.59$  ( $r^2=0.8$ ; Fig. 2). A positive linear relationship between  $f$  and  $U/L$  is similar to results reported for cetaceans, fish and other marine mammals (Bainbridge, 1958; Hunter and Zweifel, 1971; Webb and Kostecki, 1984; Feldkamp, 1987; Fish et al., 1988; Scharold et al., 1989). Regression equation for  $f$  and  $A/L$  with respect to  $U/L$  for each species is provided in Table 2. The negative slope in the regression equation for  $f$  by *G. melaena* is due to the limited speed range.

#### Strouhal data

The computed Strouhal number showed little dependence on body length or swim speed for the delphinid species (Fig. 3). Aggregating animals for each species (Fig. 4), mean  $St$  values generally reside near the lower boundary of the 0.25–0.35 range (Table 3) predicted by Triantafyllou et al. (1991, 1993)

Table 3. Mean Strouhal values

Sample size	Species	Mean $\pm$ S.D.
$n=107$	<i>Tursiops truncatus</i>	$0.26 \pm 0.05$
$n=69$	<i>Pseudorca crassidens</i>	$0.26 \pm 0.05$
$n=30$	<i>Orcinus orca</i>	$0.28 \pm 0.05$
$n=19$	<i>Delphinapterus leucas</i>	$0.35 \pm 0.1$
$n=17$	<i>Lagenorhynchus obliquidens</i>	$0.24 \pm 0.03$
$n=13$	<i>Stenella frontalis</i>	$0.33 \pm 0.03$
$n=12$	<i>Globicephala melaena</i>	$0.24 \pm 0.02$

for peak propulsive efficiency. Excluding *D. leucas*, the mean  $St$  for the delphinids was  $0.26 \pm 0.05$  ( $n=248$ ). The predicted 0.25–0.35  $St$  range captured 55% of the delphinid  $St$  data (Fig. 5), whereas the range from 0.2 to 0.3 contained 74%. For an incremental  $St$  range of 0.05, the majority of the data were found between 0.225 and 0.275 (44%). *D. leucas* had a mean  $St$  of  $0.35 \pm 0.10$  ( $n=19$ ), which was conspicuously higher than most of the  $St$  values for the delphinids.

Propulsive efficiencies, which were previously reported by Fish (1998), are plotted as a function of  $St$  in Fig. 6. For *P. crassidens*, *O. orca* and *T. truncatus*, propulsive efficiencies were found to broadly peak at about 0.90, 0.87 and 0.85, respectively, over a relatively narrow range of  $St$  (0.23–0.28). Outside this  $St$  range, where measurements exist, efficiencies drop off rapidly. The  $St$  range favored by *P. crassidens*, *O. orca* and *T. truncatus* was within this same range,  $0.225 < St < 0.30$  (Fig. 7A–C). The efficiency data for *D. leucas* were lower (0.83) and exhibit a conspicuously broader peak at  $St=0.25$ –0.40. The distribution of *D. leucas*  $St$  was relatively flat, with a narrow peak occurring at  $St=0.425$ –0.45 (Fig. 7D).

#### Discussion

Cetaceans swim by oscillatory heaving and pitching of the caudal flukes, which act as a hydrofoil (Lighthill, 1969; Webb, 1975; Fish and Hui, 1991; Fish, 1993, 1998). The oscillating movements of a hydrofoil result in unsteady shedding of vorticity from the trailing edge (Anderson et al., 1998). The pattern and spin of the staggered array of vortices generate a jet flow, which produces thrust to overcome the drag on the body. Triantafyllou et al. (1991, 1993, 2002) considered the jet to be convectively unstable, acting as a tuned amplifier with a narrow range of frequencies of maximum amplification (i.e. maximum thrust production). The pattern and periodicity of vortices shed into the wake, therefore, determine the optimal thrust production for maximum efficiency. The arrangement of vortices for maximum efficiency is a reverse

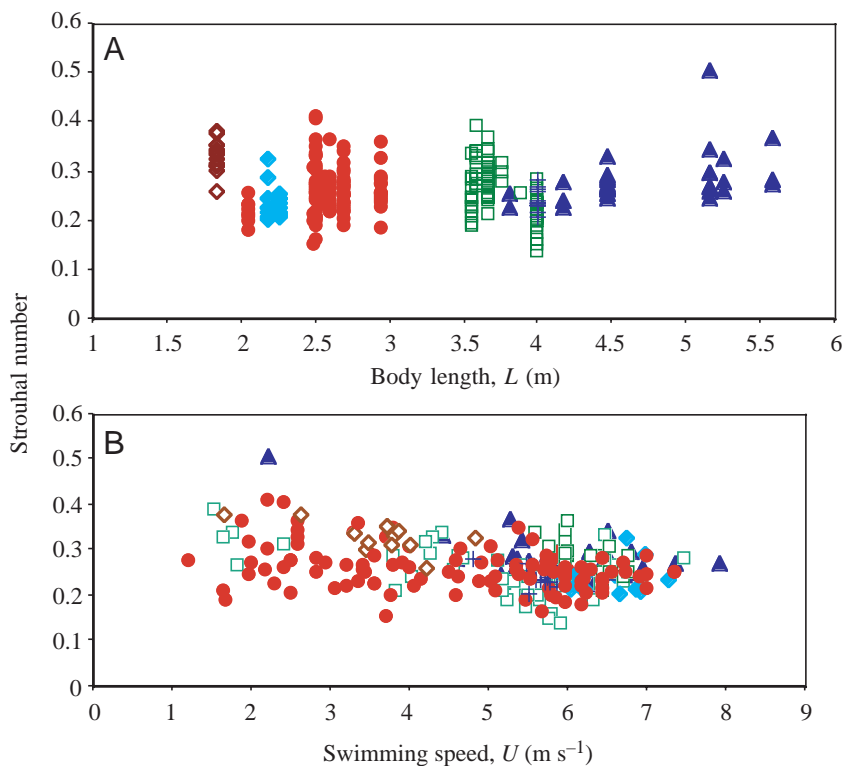


Fig. 3 (A) Strouhal number,  $St$ , of odontocete cetaceans as a function of body length,  $L$ . (B) Strouhal number,  $St$ , of odontocete cetaceans as a function of swimming speed,  $U$ . Symbols indicate particular species: *Tursiops truncatus* (solid red circles), *Pseudorca crassidens* (open green square), *Orcinus orca* (solid blue triangles), *Globicephala melaena* (blue crosses), *Lagenorhynchus obliquidens* (solid blue diamonds) and *Stenella frontalis* (open brown diamonds).

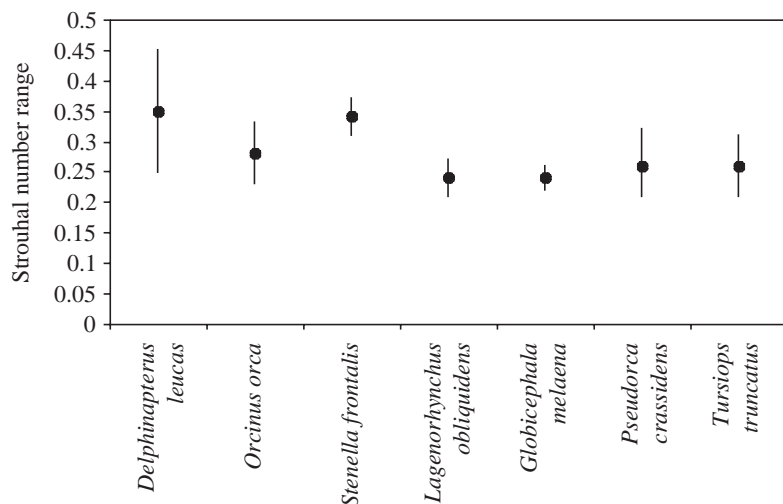


Fig. 4. Strouhal number ( $St$ ) range ( $\pm$  S.D.) for cetaceans.

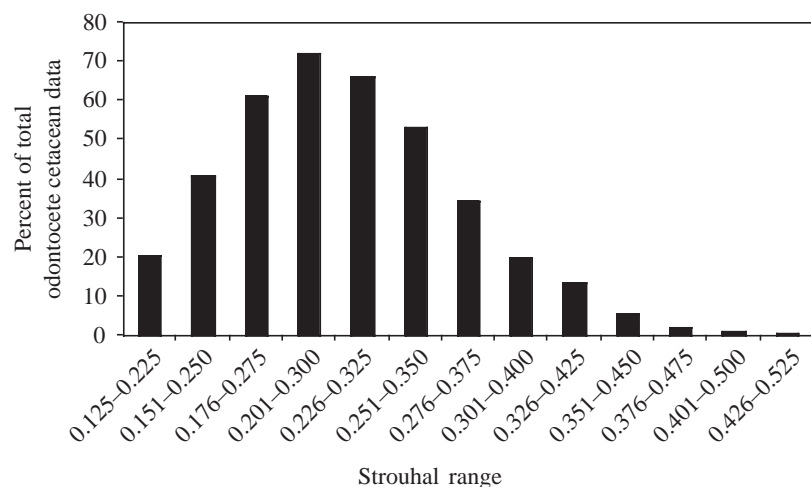


Fig. 5. Histogram of percentage of delphinid cetacean Strouhal number ( $St$ ) data ( $n=248$ ); incremental  $St$  range is 0.1, incremental step is 0.25.

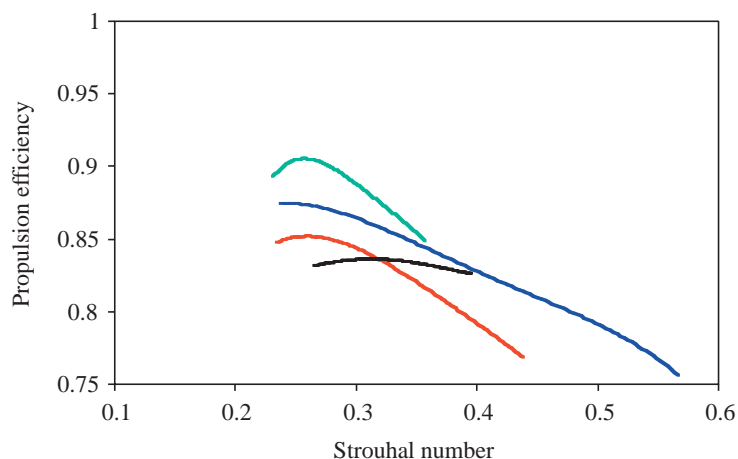


Fig. 6. Propulsion efficiency of cetaceans as a function of Strouhal number ( $St$ ). Colors indicate particular species: *Tursiops truncatus* (red), *Pseudorca crassidens* (green), *Orcinus orca* (blue) and *Delphinapterus leucas* (black).

Karman street (Triantafyllou et al., 2002). The wake dynamics are dominated by the non-dimensional Strouhal number,  $St$ , in which the distance between vortices and their rate of formation co-vary with speed (Vogel, 1994; Triantafyllou and Triantafyllou, 1995; Triantafyllou et al., 2002). Experimental studies of heaving and pitching foils have found that the structure of the vortex wake changes with  $St$  (von Ellenrieder et al., 2003; Taylor et al., 2003), maximum thrust occurred between 0.25 and 0.4 (Triantafyllou et al., 1993; Anderson et al., 1998) and maximum efficiency was within the range of 0.25–0.4 (Triantafyllou et al., 1991, 1993; Anderson et al., 1998). Efficiencies for flapping foil experiments have been reported to peak below the optimum 0.25–0.35  $St$  range predicted.

The data for all delphinids ( $n=248$ ) showed little dependence on  $St$  over a range of swim speeds from about 2–8 m s<sup>-1</sup> (Fig. 3B). It has been hypothesized for cruising flight and swimming that  $St$  would be ‘tuned’ for high propulsive efficiency (Triantafyllou et al., 1991, 1993; Taylor et al., 2003). Cruising speeds for the cetaceans have been reported from ~1–5 m s<sup>-1</sup> (see Fish, 1998). For the present  $St$  data (Fig. 5), a conspicuous peak was not apparent at cruising speeds (Fig. 3B) or where maximum propulsive efficiency was predicted ( $St=0.25$ –0.35). Moreover, the  $St$  data were not most concentrated in the predicted range. Whereas 55% of the data fell within the predicted range of  $St=0.25$ –0.35, 74% of all the  $St$  data occurred between 0.2 and 0.3. Some of the scatter in the  $St$  data is a result of measurement uncertainty. Wolfgang et al. (1999) have reported  $St$  uncertainties of ~30% for studies with fish (*Danio malabaricus*). However, a large part is presumably due to natural variation of the animal’s swimming motion (Rosen, 1959; Wolfgang et al., 1999). Kayan and Pyatetskiy (1977) reported a dependence of  $St$  on acceleration for captive *T. truncatus*, with  $St$  increasing with increasing acceleration. Taylor et al. (2003) similarly found that, for birds,  $St$  was significantly higher for intermittent as opposed to direct flight. Although data from the present video analysis were limited to steady swimming speeds, effects due to small accelerations were possible. A dependence of  $St$  on acceleration may partly explain the difference in  $St$  values for *L. obliquidens* between the present data ( $St=0.24\pm0.03$ ,  $n=17$ ) and those inferred from traces of an accelerating animal ( $St=0.30$ ,  $n=1$ ; Triantafyllou et al., 1991, 1993).

One cannot be certain that the mode of steady swimming in captivity for relatively short durations and near the water surface is similar to that employed for long durations in the wild. However, the high-speed swimming capability of regularly exercised captive and free-ranging dolphins is generally similar (Rohr et al., 2002). Pershin (1988) reports an  $St$  value of 0.37 for a free-ranging dolphin, which he refers to as a common dolphin. Pershin (1988) makes no reference to whether the animal was accelerating or how the recordings were made. Unlike the captive dolphins in the present study, this free-ranging dolphin was not swimming near the surface. Except for *D. leucas* and *S. frontalis*, an  $St$  value of 0.37 is conspicuously higher than the mean values reported here. It is not known if this disparity reflects differences between species, captive and free-ranging animals, steady or accelerated swimming or different depths beneath the surface.

A hydromechanical model of lunare-tail propulsion based on three-dimensional unsteady wing theory with continuous loading (Chopra and Kambe, 1977; Yates, 1983) was used by Fish (1998) to calculate efficiency for *O. orca*, *T. truncatus*, *P. crassidens* and *D. leucas*. Here, efficiency refers to the Froude efficiency defined as the mean rate of mechanical work derived from mean thrust, divided by all the work that the animal is performing while swimming (Chopra and Kambe, 1977). The calculated efficiencies are similar to values reported previously using different hydrodynamic models (Fish, 1998). Maximum efficiencies of 85–90% generally occurred at typical cruising speeds (Fish, 1998). Similarly, the minimum cost of transport coincides with the range of cruising speeds in *T. truncatus* (Williams et al., 1992; Yazdi et al., 1999). Efficiency values as high as 85% have been measured for advanced torpedo propellers that take advantage of the boundary layer wake (Lang and Daybell, 1963).

Dolphin efficiencies were significantly higher than values measured for conventional small rigid propellers, which are typically no more than 40% (Triantafyllou and Triantafyllou, 1995). The higher efficiencies of dolphins are probably due to some degree of  $St$  'tuning' (in 0.2  $St$  increments, 94% of the  $St$  data were between 0.2 and 0.4), oscillatory fluke motions and greater flexibility of the flukes. Oscillating foils can produce high lift coefficients and efficiencies by vorticity control (Gopalkrishnan et al., 1994; Anderson et al., 1998; Ramamurti et al., 2002; Read et al., 2003). The unsteady effects can increase the lift and permit the foil to function at high angles of attack without stalling. Cetacean flukes are lateral extensions of the tail and are a composite of flexible elements, including dense fibrous tissue,

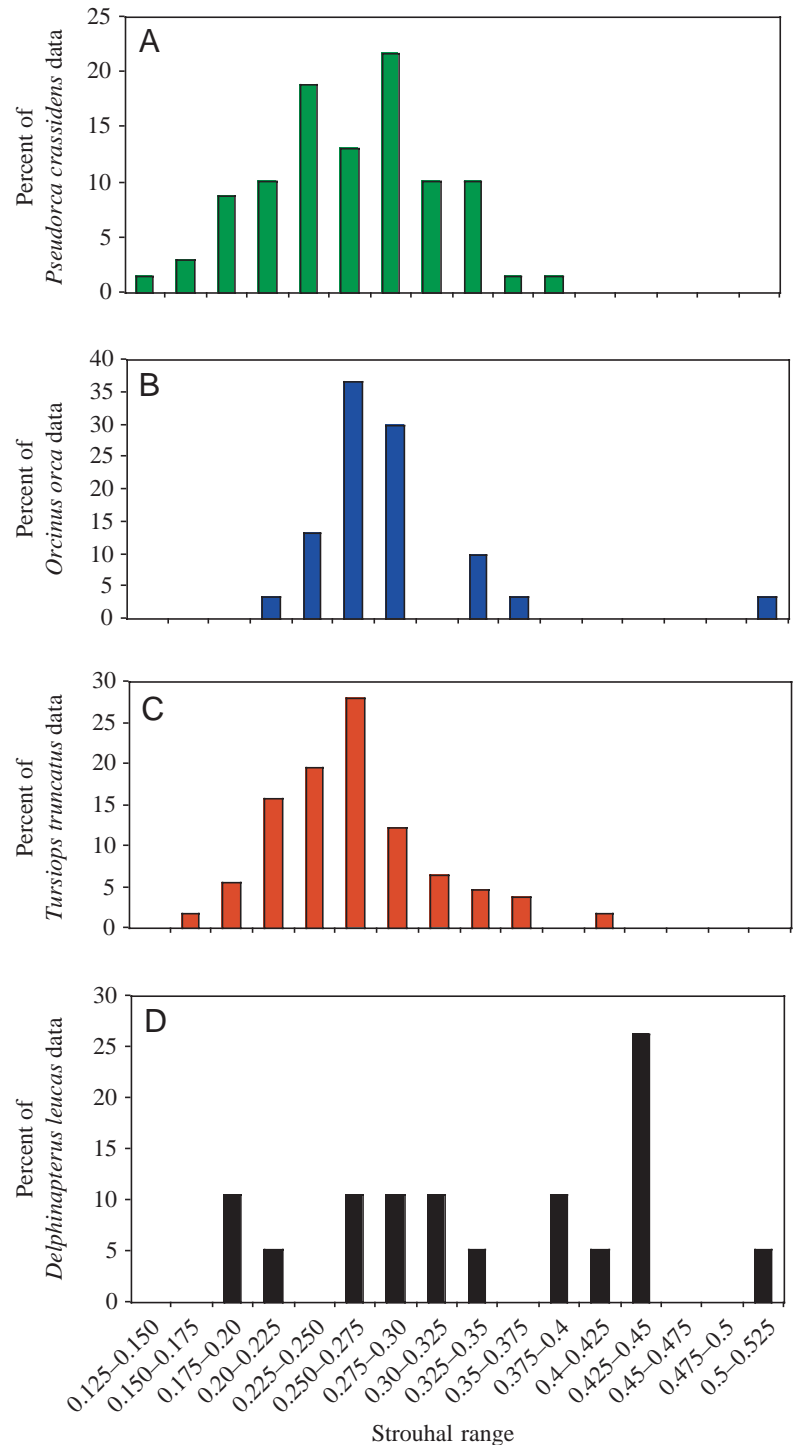


Fig. 7. Histogram of percentage of (A) *Pseudorca crassidens* ( $n=69$ ), (B) *Orcinus orca* ( $n=30$ ), (C) *Tursiops truncatus* ( $n=107$ ) and (D) *Delphinapterus leucas* ( $n=19$ ) Strouhal number ( $St$ ) data.

ligaments and blubber (Felts, 1966). The only rigid components in the cetacean tail are a series of short caudal vertebrae, which support the flukes axially (Rommel, 1990). The white-sided dolphin (*Lagenorhynchus acutus*) shows 35% and 13% chordwise and spanwise deflections, respectively (Curren et al., 1994). Chordwise flexibility of an oscillating foil



has been demonstrated experimentally and theoretically to increase efficiency by up to 36% with only a small reduction in thrust compared with a rigid foil (Katz and Weihs, 1978, 1979; Bose, 1995; Prempraneerach et al., 2003). Heaving and pitching motions of flexible foil produced a maximum efficiency of 0.87 at  $St=0.3$ , and an efficiency of 0.8 was achieved at various combinations of angles of attack around  $15^\circ$  and  $St$  ranging from 0.17 to 0.35 (Prempraneerach et al., 2003).

Prior to the present investigation there have been no studies, for either cetaceans or fish, that addressed whether swimming efficiency occurs within the predicted 0.25–0.35 range of Triantafyllou et al. (1991, 1993) (Bandyopadhyay et al., 2000). Cetacean  $St$  values occurred in the present study most frequently in the range  $0.225 < St < 0.275$  (Figs 5, 7A–C). Peak Froude efficiencies were found in this same range (Fig. 6), which straddles the lower boundary of the 0.25–0.35  $St$  range predicted. Although there are no cetacean or fish efficiency measurements to compare with, there are relevant data for two-dimensional foils. Bandyopadhyay (2002) reported the peak efficiency for a pair of tail flapping foils to be below the 0.25–0.35  $St$  range. The efficiency for oscillating foils reported by Triantafyllou et al. (1993), although maximal in the  $St$  range between 0.2 and 0.35, is practically flat. The efficiency *versus*  $St$  data of Anderson et al. (1998; Fig. 5) for a two-dimensional foil clearly do not show peak efficiencies tuned to an  $St$  range between 0.25 and 0.35. The lack of closer agreement with the present data is not surprising given that the foil experiments could not (and were not assumed to) capture the full flow field dynamics of swimming animals.

$St$  is often expressed as the product of non-dimensional peak-to-peak fluke amplitude ( $A/L$ ) and non-dimensional

frequency [ $f/(U/L)$ ]. Plotting the data in these coordinates and including contours of constant  $St$  values provides an additional perspective on the parameters controlling the range of  $St$  encountered (Fig. 8). Regardless of  $St$  value, 89% of all the  $A/L$  data ( $n=267$ ) falls within a range of 0.15–0.25. Cetaceans are known to maintain a nearly constant  $A/L$  of 0.20 with respect to  $U$  (Kayan and Pyatetskiy, 1977; Fish, 1998; Fish et al., 2003). A value of 0.20 for  $A/L$  is also typical for other animals that swim by movements of the body and tail (Bainbridge, 1958; Webb, 1975; Videler, 1993; Fish, 1998; Schultz and Webb, 2002; Fish et al., 2003).

Swim speed is controlled through frequency modulation, as is common for fish and other marine mammals that swim by oscillations of high aspect ratio hydrofoils (Bainbridge, 1958; Hunter and Zweifel, 1971; Webb and Kostecki, 1984; Feldkamp, 1987; Fish et al., 1988; Scharold et al., 1989). Regardless of  $St$  value, 90% of  $f/(U/L)$  data falls within a range of 1–2. Note, if  $A/L=0.15$ –0.25 and  $f/(U/L)=1$ –2, the corresponding  $St$  range is 0.15–0.50. Presumably the ‘boundaries’ imposed by  $A/L$  and  $f/(U/L)$  on  $St$  are manifestations of additional morphological and hydrodynamic constraints imposed on the animal. Optimal  $St$  values for pitching, heaving and flapping foils have also been found to depend on other kinematic parameters, including angle of attack, amplitude-to-chord ratio and phase of motion (Anderson et al., 1998; Wang, 2000; Bandyopadhyay et al., 2000; Read et al., 2003).

Representative  $St$  has often been estimated by simply multiplying the slope of frequency *versus* speed over length by the mean non-dimensional peak-to-peak fluke amplitude (Triantafyllou et al., 1993; Bandyopadhyay, 2002). This assumes the  $f$  *versus*  $U/L$  data passes through the origin. The slope of  $f$  *versus*  $U/L$  throughout the present data is 0.89 (Fig. 2). The mean  $A/L$  is 0.21. This product results in an estimate of 0.19 for  $St$  for odontocete cetaceans. However, if the product of  $f/(U/L)$  and  $A/L$  is first calculated for each observation and then averaged,  $St=0.27$ . A 30% disparity results because the y-intercept (0.58; see Fig. 2) of the least squares estimate of  $f$  *versus*  $U/L$  was initially ignored.

Whereas 91% of all the cetacean data fall between  $St=0.2$  and 0.4, a significant fraction (37%) of the *D. leucas* data conspicuously fell outside this range. Mean  $St$  for *D. leucas* is  $0.35 \pm 0.10$  compared with  $0.27 \pm 0.06$  for the other cetaceans examined in this study. It has been noted that the swimming performance and efficiency of *D. leucas* differ considerably from those of other cetaceans, which is consistent with its general body contour and low aspect ratio flukes (Fish, 1998). *D. leucas* generally exhibits the poorest swimming performance of cetaceans. This species feeds on slow-moving prey, including crustaceans and annelids (Brodie, 1989). The mean  $St$  for *S. frontalis* was also high at  $0.33 \pm 0.03$ . Unlike *D. leucas*, *S. frontalis* is a fast swimmer (Fish and Rohr, 1999). The individual *S. frontalis* examined in this study had a mean  $A/L$  of  $0.25 \pm 0.02$ , which was the highest of any species tested.

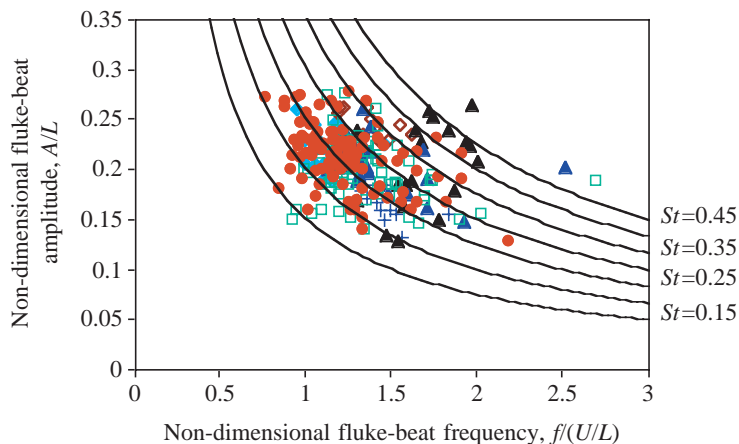


Fig. 8. Non-dimensional fluke-beat amplitude,  $A/L$ , as a function of non-dimensional fluke-beat frequency,  $f/(U/L)$ , where  $A$  is the peak-to-peak fluke amplitude,  $L$  is the body length,  $f$  is the fluke-beat frequency and  $U$  is the swimming speed. Contours of constant Strouhal number,  $St$ , are included. Symbols indicate particular cetacean species: *Tursiops truncatus* (solid red circles), *Pseudorca crassidens* (open green squares), *Orcinus orca* (solid blue triangles), *Globicephala melaena* (blue crosses), *Lagenorhynchus obliquidens* (solid blue diamonds), *Stenella frontalis* (open brown diamonds) and *Delphinapterus leucas* (solid black triangles).

The data presented in this study significantly expand the previously used Strouhal data for cetaceans (Triantafyllou et al., 1991, 1993; Triantafyllou and Triantafyllou, 1995; Taylor et al., 2003) by greatly increasing the number of observations (more than 100-fold), species (7-fold) and range of Reynolds number (10-fold) and, for the first time, provide a direct comparison between measured Strouhal number and swimming efficiency. The present data show that over the range of swim speeds observed,  $2\text{--}8\text{ m s}^{-1}$ , cetaceans swim at  $St$  values between 0.2 and 0.4, preferring a range of 0.2–0.3 where maximum efficiencies occur. The strong relationship between maximum propulsive efficiency and  $St$  continues to support the premise (Triantafyllou et al., 1991, 1993) that vorticity control associated with fluke kinematics is an important attribute of cetacean swimming performance.

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## References

- Anderson, J. M., Streitlien, K., Barrett, D. S. and Triantafyllou, M. S. (1998). Oscillating foils of high propulsive efficiency. *J. Fluid Mech.* **360**, 41–72.
- Bainbridge, R. (1958). The speed of swimming of fish as related to size and to frequency and amplitude of the tailbeat. *J. Exp. Biol.* **35**, 109–133.
- Bandyopadhyay, P. R., Krol, W. P., Jr, Thivierge, D. P., Nedderman, W. H. and Mojarad, M. (2000). A biomimetic propulsor for active noise control. Part 1: Experiments. *Bull. Am. Phys. Soc.* **45**, No. 9:95.
- Bandyopadhyay, P. R. (2002). Maneuvering hydrodynamics of fish and small underwater vehicles. *Integ. Comp. Biol.* **42**, 102–117.
- Bose, N. (1995). Performance of chordwise flexible oscillating propulsors using a time-domain panel method. *Int. Shipbuild. Progr.* **42**, 281–294.
- Brodie, P. F. (1989). The white whale *Delphinapterus leucas* (Pallas, 1776). In *Handbook of Marine Mammals*, vol. 4 (ed. S. H. Ridgway and R. Harrison), pp. 119–144. London: Academic Press.
- Chopra, M. G. and Kambe, T. (1977). Hydrodynamics of lunate-tail swimming propulsion. Part 2. *J. Fluid Mech.* **79**, 49–69.
- Curren, K. C., Bose, N. and Lien, J. (1994). Swimming kinematics of a harbor porpoise (*Phocoena phocoena*) and an Atlantic white-sided dolphin (*Lagenorhynchus acutus*) *Mar. Mamm. Sci.* **10**, 485–492.
- Feldkamp, S. D. (1987). Foreflipper propulsion in the California sea lion, *Zalophus californianus*. *J. Zool. Lond.* **212**, 43–57.
- Felts, W. J. L. (1966). Some functional and structural characteristics of cetaceans flippers and flukes. In *Whales, Dolphins and Porpoises* (ed. K. S. Norris), pp. 255–276. Berkeley: University of California Press.
- Fish, F. E. (1993). Power output and propulsive efficiency of swimming bottlenose dolphins (*Tursiops truncatus*). *J. Exp. Biol.* **185**, 179–193.
- Fish, F. E. (1998). Biomechanical perspective on the origin of cetacean flukes. In *The Emergence of Whales: Evolutionary Patterns in the Origin of Cetacea* (ed. J. G. M. Thewissen), pp. 303–324. New York: Plenum.
- Fish, F. E. and Hui, C. A. (1991). Dolphin swimming – A review. *Mamm. Rev.* **21**, 181–195.
- Fish, F. E. and Rohr, J. (1999). Review of dolphin hydrodynamics and swimming performance. *SPAWARS System Center Technical Report 1801*, San Diego, CA. <http://www.spawar.navy.mil/sti/publications/pubs/tr1801/tr1801.pdf>.
- Fish, F. E., Innes, S. and Ronald, K. (1988). Kinematics and estimated thrust production of swimming harp and ringed seals. *J. Exp. Biol.* **137**, 157–173.
- Fish, F. E., Peacock, J. E. and Rohr, J. J. (2003). Stabilization mechanism in swimming odontocete cetaceans by phased movements. *Mar. Mamm. Sci.* **19**, 515–528.
- Gopalkrishnan, R., Triantafyllou, M. S., Triantafyllou, G. S. and Barrett, D. (1994). Active vorticity control in a shear flow using a flapping foil. *J. Fluid Mech.* **274**, 1–21.
- Hunter, J. R. and Zweifel, J. R. (1971). Swimming speed, tail beat frequency, tail beat amplitude, and size in the jack mackerel *Trachurus symmetricus*, and other fishes. *Fish. Bull.* **69**, 253–266.
- Katz, J. and Weihs, D. (1978). Hydrodynamic propulsion by large amplitude oscillation of an airfoil with chordwise flexibility. *J. Fluid Mech.* **88**, 485–497.
- Katz, J. and Weihs, D. (1979). Large amplitude unsteady motion of a flexible slender propulsor. *J. Fluid Mech.* **90**, 713–723.
- Kayan, Y. P. and Pyatetskiy, V. Ye. (1977). Kinematics of bottlenose dolphins swimming as related to acceleration mode. *Bionika* **11**, 36–41.
- Lang, T. G. and Daybell, D. A. (1963). Porpoise performance tests in a seawater tank. *Nav. Ord. Test Sta. Tech. Rep.* **3063**, 1–50.
- Lighthill, M. J. (1969). Hydrodynamics of aquatic animal propulsion – a survey. *Annu. Rev. Fluid Mech.* **1**, 413–446.
- Pershin, S. V. (1988). *Fundamentals of Hydrobionics*. Leningrad: Sudostroyeniye House.
- Prempraneerach, P., Hover, F. S. and Triantafyllou, M. S. (2003). The effect of chordwise flexibility on the thrust and efficiency of a flapping foil. In *Proceedings of the Thirteenth International Symposium on Unmanned Unethered Submersible Technology: Proceedings of the Special Session on Bio-Engineering Research Related to Autonomous Underwater Vehicles*. Lee, New Hampshire: Autonomous Undersea Systems Institute.
- Pyatetskiy, V. Ye. (1970). Kinematic swimming characteristics of some fast marine fish. *Bionika* **4**, 12–23.
- Ramamurti, R., Sandberg, W. C., Lohner, R., Walker, J. A. and Westneat, M. W. (2002). Fluid dynamics of flapping aquatic flight in the bird wrasse: three-dimensional unsteady computations with fin deformation. *J. Exp. Biol.* **205**, 2997–3008.
- Read, D. A., Hover, F. S. and Triantafyllou, M. S. (2003). Forces on oscillating foils for propulsion and maneuvering. *J. Fluids Struct.* **17**, 163–183.
- Rohr, J. J., Fish, F. E. and Gilpatrick, J. W., Jr (2002). Maximum swim speeds of captive and free-ranging dolphins: critical analysis of extraordinary performance. *Mar. Mamm. Sci.* **18**, 1–19.
- Rommel, S. (1990). Osteology of the bottlenose dolphin. In *The Bottlenose Dolphin* (ed. S. Leatherwood and R. R. Reeves), pp. 29–49. New York: Academic Press.
- Rosen, M. W. (1959). Water flow about a swimming fish. *US Nav. Ord. Test Sta. Tech. Pub.* **2298**, 1–96.
- Rosen, M. W. (1961). Experiments with swimming fish and dolphins. *Publication 61-WA-203, 1-11*. New York: American Society of Mechanical Engineers.
- Rosen, M. W. (1963). Flow visualization experiments with a dolphin. *US Nav. Ord. Test Sta. Tech. Pub.* **8062**, 1–14.
- Scharold, J., Lai, N. C., Lowell, W. R. and Graham, J. B. (1989). Metabolic rate, heart rate and tailbeat frequency during sustained swimming in the leopard shark *Triakis semifasciata*. *Exp. Biol.* **48**, 223–230.
- Schultz, W. W. and Webb, P. W. (2002). Power requirements of swimming: do new methods resolve old questions? *Integ. Comp. Biol.* **42**, 1018–1025.
- Semonov, N. P., Babenko, V. V. and Kayan, V. P. (1974). Experimental research on some features of dolphin swimming hydrodynamics. In *Dolphin Propulsion, Echolocation Research, Bionika*, no. 8. Kiev, USSR: Izd-vo Nauvova Dumka.
- Streitlien, K. and Triantafyllou, G. S. (1998). On thrust estimates for flapping foils. *J. Fluid Struct.* **12**, 47–55.
- Taylor, G. K., Nudds, R. L. and Thomas, A. L. R. (2003). Flying and swimming animals cruise at a Strouhal number tuned for high power efficiency. *Nature* **425**, 707–711.
- Triantafyllou, G. S. and Triantafyllou, M. S. (1995). An efficient swimming machine. *Sci. Am.* **272**, 40–48.
- Triantafyllou, M. S., Triantafyllou, G. S. and Gopalkrishnan, R. (1991). Wake mechanics for thrust generation in oscillating foils. *Phys. Fluids* **3**, 2835–2837.
- Triantafyllou, G. S., Triantafyllou, M. S. and Grosenbaugh, M. A. (1993). Optimal thrust development in oscillating foils with applications to fish propulsion. *J. Fluid Struct.* **7**, 205–224.

- Triantafyllou, M. S., Triantafyllou, G. S. and Yue, D. K. P.** (2000). Hydrodynamics of fishlike swimming. *Annu. Rev. Fluid Mech.* **32**, 33-53.
- Triantafyllou, M. S., Techet, A. H., Zhu, Q., Beal, D. N., Hover, F. S. and Yue, D. K. P.** (2002). Vorticity control in fish-like propulsion and maneuvering. *Integ. Comp. Biol.* **42**, 1026-1031.
- Videler, J. J.** (1993). *Fish Swimming*. London: Chapman and Hall.
- Vogel, S.** (1994). *Life in Moving Fluids*. Princeton, NJ: Princeton University Press.
- von Ellenrieder, K. D., Parker, K. and Soria, J.** (2003). Flow structures behind a heaving and pitching finite-span wing. *J. Fluid. Mech.* **490**, 129-138.
- Wang, Z. J.** (2000). Vortex shedding and frequency selection in flapping flight. *J. Fluid Mech.* **410**, 323-341.
- Webb, P. W.** (1975). Hydrodynamics and energetics of fish propulsion. *Bull. Fish. Res. Bd. Can.* **190**, 1-158.
- Webb, P. W. and Kostecki, P. W.** (1984). The effect of size and swimming speed on locomotor kinematics of rainbow trout. *J. Exp. Biol.* **109**, 77-95.
- Williams, T. M., Friedl, W. A., Fong, M. L., Yamada, R. M., Sedivy, P. and Haun, J. E.** (1992). Travel at low energetic cost by swimming and wave-riding bottlenose dolphins. *Nature* **355**, 821-823.
- Wolfgang, M. J., Anderson, J. M., Grosenbaugh, M. A., Yue, D. K. P. and Triantafyllou, M. S.** (1999). Near-body flow dynamics in swimming fish. *J. Exp. Biol.* **202**, 2303-2327.
- Yazdi, P., Kilian, A. and Culik, B.** (1999). Energy expenditure of swimming bottlenose dolphins (*Tursiops truncatus*). *Mar. Biol.* **134**, 601-607.
- Yates, G. T.** (1983). Hydrodynamics of body and caudal fin propulsion. In *Fish Biomechanics* (ed. P. W. Webb and D. Weihs), pp. 177-213. New York: Praeger.
- Zar, J. H.** (1984). *Biostatistical Analysis*. Second edition. Englewood Cliffs, NJ: Prentice Hall.